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Abstract

In species with sexual size dimorphism, offspring of the larger sex usually have greater energy requirements and may lead to greater fitness costs for parents. The effects of offspring sex on maternal longevity, however, have only been tested in humans. Human studies produced mixed results and considerable debate mainly due to the difficulty of distinguishing the effects of sexual dimorphism from sociocultural factors. To advance this debate, we examined how the relative number of sons influenced maternal longevity in four species of free-living ungulates (Soay sheep *Ovis aries*; bighorn sheep, *Ovis canadensis;* red deer, *Cervus elaphus*; mountain goat, *Oreamnos americanus*), with high male-biased sexual size dimorphism but without complicating sociocultural variables. We found no evidence for a higher cumulative cost of sons than of daughters on maternal longevity. For a given number of offspring, most females with many sons in all four populations lived longer than females with few sons. The higher cost of sons over daughters on maternal lifespan reported by some human studies may be the exception rather than the rule in long-lived iteroparous species.

Keywords: cost of reproduction, disposable soma, lifespan, mammals, sex ratio, trade-offs.

1. Introduction

Trade-offs play a fundamental role in life-history theory [1]. Organisms allocate acquired energy among several functions including growth, reproduction and maintenance. When resources are limited, energy allocated to one function reduces allocation to others [2]. Therefore, increasing reproductive effort should reduce the energy available for somatic maintenance, possibly decreasing longevity [3]. Because longevity is a major source of variation in lifetime reproductive success and fitness among long-lived species [4], knowledge of the processes driving variation in longevity is essential to understand population dynamics and evolutionary ecology.

Longevity costs of reproduction may vary with sex of both parents [5] and offspring [6]. Sex differences in energy intake and growth of juveniles are common in sexually size-dimorphic species [7]. In humans, despite weak sexual dimorphism [8], the energy intake of pregnant women is about 10% higher when they are expecting a boy rather than a girl [9]. In dimorphic species where sons grow faster than daughters and thus require greater parental energy expenditure, the fitness costs of rearing sons are typically expected to be greater than those of rearing daughters [7]. In many mammals, only mothers provide parental care, and there is suggestive evidence that short-term fitness costs of reproduction (how reproduction at time t affects survival or reproduction at time $t + 1$) are greater for females when rearing a son than a daughter [10–17]. Most of these studies are indicative rather than conclusive because correlation does not imply causation. Experimental manipulation of postnatal offspring sex ratio has only been performed in bank voles (*Myodes glareolus*) [17,18] and tammar wallabies (*Macropus eugenii*) [19,20]. This type of experiment is unfortunately impracticable with most mammals, in part due to maternal refusal of cross-fostered offspring [20].

Beyond short-term fitness costs of reproduction, the accumulation of physiological costs over multiple reproductive events may have long-term effects on future performance

[3,21]. Most studies testing early-late life trade-offs measured early reproductive effort as the number of offspring produced or reared during a predefined time period [21], ignoring offspring sex. Thus, we know little about the long-term cumulative fitness costs to females of producing and rearing sons versus daughters. The only exceptions are investigations in humans, which provide mixed support for the hypothesis that sons reduce maternal post-menopausal lifespan more than daughters (see mini-review in [22]). Furthermore, the differential effects of sons and daughters on post-reproductive lifespan in human mothers may be due to sociocultural rather than biological mechanisms [23–25]. For instance, in several societies, daughters provide more help than sons for elderly parents [25,26].

Here, we examine the long-term impact of producing and rearing more sons relative to daughters on maternal longevity in four intensively monitored populations of free-living ungulates: Soay sheep (*Ovis aries*), bighorn sheep (*Ovis canadensis*), red deer (*Cervus elaphus*) and mountain goat (*Oreamnos americanus)*. These species show a marked male-biased sexual size dimorphism and a relatively simple social system compared to humans. In all species except Soay sheep, rearing a son lowers maternal reproductive performance the following year more than rearing a daughter [11,13,27,28]. We expected to find a negative effect of producing and rearing relatively more sons than daughters on maternal longevity, especially in bighorn sheep, red deer and mountain goats.

2. Materials and Methods

(a) Study populations

We studied bighorn sheep at Ram Mountain (38 km²) and mountain goats at Caw Ridge (28 km²), Alberta, Canada. The red deer and Soay sheep populations are respectively located in the North Block (12 km²) of the Isle of Rum and in the Village Bay area (2.3 km²) on the

island of Hirta, St Kilda, both off the west coast of Scotland, UK. Study areas are unfenced and thus open to movements, but female dispersal is rare in all four populations [29–32].

(b) Capturing and marking

The study populations have been the subject of detailed individual-based monitoring for 3 or 4 decades (table 1). For all species except mountain goats, most individuals were first captured, weighed, sampled for genetic analysis, and marked near birth. Female bighorn sheep, red deer and mountain goats can produce a single offspring in May-June. Female Soay sheep can give birth to either singletons or twins in March-April (mean twinning rate 15%, [33]). In red deer and Soay sheep, all females are monitored for parturition on a daily basis during the spring, and offspring are caught within a few days of birth. In bighorn sheep, age at first capture in a corral trap varies from 1 week to 4 months, but most are captured within a few weeks of birth. Since 1998, female goats with their offspring are not captured owing to the risk of abandonment, so most individuals are aged 1 year or older when first caught in box traps [34]. The age of female mountain goats not marked as yearlings (1 year old) was determined by counting the number of horn annuli, a technique reliable up to 7 years of age [32]. Animals are marked with colored ear tags and/or visual collars for individual identification at a distance (fig. S1 in electronic supplementary information). Techniques used to capture, mark and monitor individuals are described in detail elsewhere [32,33,35,36].

(c) Longevity

Regular censuses of the study areas are conducted from May to September for bighorn sheep and mountain goats and throughout the year for red deer and Soay sheep. Longevity for red deer and Soay sheep is based on the date an animal was found dead in ~ 70 and 85% of cases or on date of last sighting in the remaining cases [33,36]. In bighorn sheep and mountain goats, 1 and 17% of carcasses were found respectively but the date of last sighting is a reliable indicator of age at death since there is almost no record of female emigration [32,37]. The

annual likelihood of missing a female if she is alive is very low in all systems (re-sighting probability: 0.99 for both bighorn sheep [29] and mountain goats [32], 0.95 for red deer [30], and 0.93 for Soay sheep [31]). Our analyses included only resident females that reproduced at least once before natural death (excluding hunter kills in red deer, removals for scientific purposes and capture mortalities). Possible causes of natural mortality included starvation [38] especially at high population density, adverse weather, parasitism, disease, as well as predation in bighorn sheep [39] and mountain goats [32].

(d) Reproduction

Intensive observations took place every summer to determine mother-offspring associations and offspring survival. Weaning success was measured by offspring survival to 15 September in bighorn sheep and mountain goats, 1 August in Soay sheep and 1 October in red deer. Although mountain goat kids were not marked, they tightly follow and bed next to their marked mothers, providing an accurate determination of their fate until weaning, and often until one year old ([32] and fig. S1). In mountain goats, offspring sex was determined by observations of urination posture and the vulvar patch in females. In the other species, offspring sex was determined at capture or, occasionally, through observation of urination posture.

(e) Models

We ran two types of models to examine the effects of sons on maternal longevity. First, in the context of early-late life trade-offs, we assessed whether the number of sons born and weaned during early life influenced maternal lifespan later in life. We defined 'early life' at the population level as between minimum age at first parturition and age at onset of actuarial senescence (see [40,41] for a similar approach and table 1 for definition of actuarial senescence). 'Early life' overlapped the latest age at which any females started breeding (table 1). Actuarial senescence is well documented in all four populations [30–32,42]. We only

included females that survived beyond the onset of actuarial senescence in this first approach (see tables 2 and 3 for sample sizes). Second, we examined correlations between the lifetime number of sons born or weaned and maternal longevity using all data (see tables 4 and 5 for sample sizes). The reasons for this second approach include the fact that longevity costs of producing and rearing sons may not be confined to older mothers [43]. The proportion of sons produced or weaned, on average, during early life or lifetime is presented in the electronic supplementary information, table S1.

In all models, we controlled for the number of offspring produced/weaned during early life or lifetime. Thus, we investigated whether for females with the same number of offspring, having more sons affected longevity, thereby accounting for variation in reproductive potential that may mask costs of sons. In Soay sheep, we accounted for the number of twin pairs because females that produced twins tended to died younger [44]. Our models included interactions between the number of offspring and the number of sons because costs of reproduction may be greater in females with lower reproductive potential [45–47]. We tested the effects of both the number of offspring born and weaned on maternal longevity to determine the importance of gestation and lactation in generating reproductive costs.

All analyses were performed in R (ver. 3.5.0) [48]. Maternal longevity was analyzed in generalized linear mixed models with the package 'glmmTMB' [49], using the Conway-Maxwell-Poisson distribution to deal with under-dispersion [50]. The distribution of longevity for each species is shown in figure S2. Year of birth was included as a random effect to account for non-independence of mothers born in the same year and variation in longevity among cohorts. Females were born between 1973 and 2004 in bighorn sheep, 1984 and 2003 in mountain goats, 1968 and 2004 in red deer, and 1985 and 2007 in Soay sheep. Regression coefficients (β) and their standard errors (SE) are shown for all fixed covariates, along with statistical significance based on Wald Z statistic. To assess effect sizes, we reported

155 standardized regression coefficients obtained by centring and scaling all continuous
156 explanatory variables (mean = 0, variance = 1). Centring enables interpretation of the main
157 effects involved in an interaction [51]. Thus, we presented the estimates and SE from full
158 models [52]. Variance inflation factors for all explanatory variables in our models were less
159 than 5, indicating no multicollinearity problems [53].

160 ***(f) Multiple imputation***

161 The sex of each offspring born was known for most, but not all, female-years (68% in bighorn
162 sheep, 90% in mountain goats, 94% in red deer, 97% in Soay sheep; see table 1 for raw
163 numbers). In bighorn sheep, the sex of lambs that died at birth or within a few days of birth
164 was unknown because no lamb was seen but milk or colostrum was expressed by the mother
165 at capture. Yearly weaning success of female red deer and Soay sheep was missing in 6% and
166 2% of cases. We used multiple imputation to predict these two kinds of missing values. We
167 created multiple "complete" datasets where the missing values were imputed based on
168 information from all variables in the dataset. We used multiple imputation by chained
169 equation (function mice in the package 'mice', [54]) because this method is robust and allows
170 categorical variables to be imputed [55]. Differences in the imputed values between the
171 multiple datasets reflect imputation uncertainty. We generated ten imputed datasets for each
172 species as recommended by [56], and calculated the number of sons born/weaned in each
173 dataset. We obtained ten different estimates and their standard errors for each effect of
174 producing/weaning sons (one from each imputed dataset) and used conventional multiple
175 imputation rules for combining results [57]. When comparing the relationships between early-
176 life reproduction and longevity in later life obtained by multiple imputation with those from
177 datasets in which all females with missing values were excluded, we obtained similar patterns
178 (table S2 and S3). In the main text, we only present results based on multiple imputations

because of greater statistical power and the risk of biasing effect sizes when excluding missing values [58].

3. Results

(a) Early-life reproduction and lifespan later in life

In Soay sheep, we found an interaction between the number of offspring and sons weaned during early life on later life span ($\beta = 0.024 \pm 0.008$, $P = 0.002$) and there was a similar, though non-significant, interaction between the number of offspring and sons born (rather than weaned, $\beta = 0.016 \pm 0.009$, $P = 0.09$). The relationship between number of sons and maternal lifespan was increasingly negative as number of lambs produced/weaned during early life decreased (fig. 1). However, the cost of sons in terms of subsequent longevity was small and not statistically significant even for females that produced ≤ 5 lambs (post-hoc analysis: $\beta = -0.021 \pm 0.005$, $P = 0.16$, $N = 176$) or weaned ≤ 4 lambs ($\beta = -0.016 \pm 0.015$, $P = 0.29$, $N = 175$) during early life. There were no significant interactions between the number of offspring and sons born or weaned in any other species (tables 2 and 3). In all species except mountain goats, the number of offspring produced during early life was positively associated with lifespan later in life (table 2). For a given number of offspring born, female bighorn sheep, red deer and mountain goats with many sons did not die sooner or later than females with few sons (table 2). Repeating the analysis using the number of sons weaned did not change the results except in bighorn sheep where the positive estimate was slightly stronger and more precise, resulting in confidence intervals that did not overlap 0 (table 3). For bighorn females that weaned 3 lambs during early life (the observed mean), longevity later in life increased from 10.2 to 12.2 years as the number of sons weaned increased from 0 to 3.

(b) Lifetime reproduction and adult lifespan

In all species, we found significant interactions between the lifetime number of offspring and sons on adult longevity regardless of whether reproductive performance was measured at birth (table 4) or weaning (table 5). All these interactive effects acted in the same direction: the relationship between number of sons and maternal longevity was increasingly positive as number of offspring produced/weaned during lifetime decreased (fig. 2). Post-hoc analyses did not show a negative effect of sons on longevity for females producing ≥ 10 offspring in Soay sheep (β = -0.004 ± 0.010, P = 0.70, N = 94) or ≥ 8 offspring in mountain goats (β = -0.011 ± 0.038, P = 0.78, N = 19) and red deer (β = 0.003 ± 0.011, P = 0.79, N = 114).

4. Discussion

Our study tested for a trade-off between cumulative reproductive effort, incorporating offspring number and sex ratio, and maternal longevity in non-human animals. Helle and colleagues showed that post-menopausal longevity of pre-industrial Sami women decreased by 0.65 years for each son born, while it increased by 0.44 years for each daughter [6]. However, the generality of these findings in pre-industrial humans has been questioned [59,60]. Cesarini and co-workers warned of widespread publication bias in favor of positive results in this area and pointed out the need for more replication studies on independent samples [61]. Our analyses of four intensively monitored populations of free-living ungulates do not support higher costs of sons than daughters to maternal lifespan.

Our study is based on correlational evidence: we could not manipulate offspring sex ratio. Thus, the positive relationship between the relative number of sons weaned during early life and maternal longevity in bighorn sheep may reflect the influence of physiological or genetic factors on these two variables, rather than causation *per se*. Although evolutionary theories of ageing predict that early allocation to reproduction should be favored by natural selection at the cost of reduced late-life traits [3,62], trade-offs are often not visible in

228 correlational studies because individuals vary in resource acquisition [63]. According to the
229 van Noordwijk and De Jong [64] model, trade-offs between life-history traits should be
230 apparent only when inter-individual variation in resource allocation exceeds variation in
231 resource acquisition. The variation in reproductive potential (often referred to as "quality",
232 [65]) that results from variation in resource acquisition may therefore mask the fitness costs of
233 reproduction at the population level [66]. In our study, some females combined a high
234 reproductive success during early life with long lifespans, whereas others had few offspring
235 and relatively short lifespans, suggesting large differences in individual reproductive
236 potential. We found no evidence for a negative effect of number of sons during early life on
237 subsequent maternal longevity even after accounting for differences in the number of
238 offspring. Nevertheless, other characteristics that affect the amount of resources available to
239 individuals, such as metabolic efficiencies [64] and social rank [67], may explain why we
240 failed to find any negative associations between the number of sons and maternal longevity.

241 We examined the effects of number of sons during early life on maternal longevity,
242 using data from females that survived beyond the onset of actuarial senescence. Recent
243 simulations [43] showed that restricting analyses to post-menopausal women underestimates
244 the potential trade-off between reproduction and lifespan. Our second approach avoids
245 potential sample selection problems by considering all adult females. These analyses
246 produced positive rather than negative correlations between the lifetime number of sons and
247 maternal longevity.

248 It could be argued that the overall lack of association between relative number of sons
249 and maternal longevity was due to a lack of statistical power in our analyses. However, our
250 sample size, at least in red deer and Soay sheep, was comparable to that in the study on
251 preindustrial Sami women that found a longevity cost of sons [6]. To maximize sample sizes,
252 we used multiple imputation to handle missing values for females with incomplete

253 reproductive histories. Unlike data deletion where cases containing at least one missing value
254 are excluded from the analysis, multiple imputation neither produces biased parameter
255 estimates nor reduces statistical power [58]. We also chose not to apply corrections for
256 multiple testing because Bonferroni and similar methods reduce statistical power and there is
257 no consensus for when multiple-testing adjustment is necessary [68,69]. We therefore believe
258 it is unlikely that lack of statistical power could explain the absence of positive results.

259 Differences in the energetic costs of sons and daughters are not necessarily limited to
260 the period of offspring nutritional dependence. In mammals, daughters are usually less prone
261 to disperse than sons [70], and are therefore more likely to compete for resources with their
262 mothers after nutritional independence [71]. In red deer on Rum, daughters typically occupy
263 core areas overlapping that of their mother and resource competition between female relatives
264 reduced the reproductive success of adult females [72]. Although the higher energetic costs of
265 sons before weaning might be balanced by post-weaning competition with daughters in red
266 deer [7], we can discard this explanation in other species. The social system of sheep does not
267 include strong post-weaning mother-daughter association [73,74]. In mountain goats, mother-
268 yearling associations were common but a recent study suggests that the post-weaning costs of
269 sons exceed those of daughters [27]. The likelihood of "helping" by one sex of mature
270 offspring may influence maternal longevity in some mammals. In pre-industrial human
271 societies, daughters typically helped in domestic and caregiving responsibilities while sons
272 simply increased maternal workload by working outside the home but living with parents
273 [75]. This sociocultural sexual division of labor offers an alternative explanation for
274 differential effects of sons and daughters on maternal longevity that are often attributed to sex
275 differences in offspring demand during pregnancy [24,75]. One advantage of our study
276 species is that offspring do not help mothers rear the next progeny.

277 There are at least two mechanisms by which females can recover from the higher
278 energetic costs of rearing sons in the short term to avoid cumulating these costs. First, females
279 can take reproductive pauses when their body reserves are insufficient. All the species studied
280 here are capital breeders that use stored energy for reproduction in contrast to income
281 breeders that rely on short-term food acquisition to finance reproduction [76]. There is
282 evidence in red deer that reproductive pauses depend on the sex of the previous offspring.
283 Indeed, female red deer that gave birth to a son are less likely to give birth the following
284 spring than mothers that had a daughter [13]. Although this effect accounted for only 1% of
285 the total variation in hind fecundity [13], it was primarily observed in low ranking mothers
286 [12]. In bighorn sheep, lambs born the year following the weaning of a son had lower survival
287 to weaning than lambs born after a daughter, particularly at high density [11]. Second,
288 mothers with low capacity to provide care, either because of low body condition, social status,
289 or experience, may produce the cheaper sex to reduce fitness costs [12,77,78]. For example,
290 the year after weaning a son bighorn sheep females in poor condition were more likely to
291 produce a daughter than a son [77].

292 A review of empirical studies of free-living mammals [79] reported that short-term
293 survival costs of reproduction are infrequent in ungulates, which exhibit high reproductive
294 variability and low variance in adult survival. Our results suggest that this pattern also holds
295 for cumulative costs of reproduction. Future studies of other groups of mammals (*e.g.* non-
296 human primates, elephants, marsupials) are needed before we can conclude that the higher
297 cost of sons over daughters on maternal longevity reported by some human studies is the
298 exception rather than the rule in long-lived mammal species. Detailed longitudinal data on
299 short-lived species, such as rodents, are also needed to test whether higher cumulative costs of
300 rearing sons on maternal longevity are more likely to be found in short-lived than long-lived
301 species.

Ethics. Ethical approval for the research on Rum's red deer and Soay sheep has been granted by the appropriate UK Home Office licences. The marking and handling of bighorn sheep at Ram Mountain and mountain goats at Caw Ridge were approved by the Animal Care Committee of the Université de Sherbrooke (protocols MFB2009-01 and FP2012-01) and the Université Laval (protocols 115513, 2018-033), both affiliated to the Canadian Council on Animal Care.

Data accessibility. Data used in this paper are available in Dryad (doi:10.5061/dryad.p0544hn).

Competing interests. We declare we have no competing interests.

Author's contributions. MD conceived the study and conducted all analyses with inputs from all co-authors. All authors edited the manuscript, provided critical reviews and gave final approval for submission.

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528 **Table captions**

529 Table 1. The four study populations of female ungulates. Age-related variation in survival is
530 well documented in each population [30–32,42]. Survival rates are high and constant for adult
531 females, then decrease after species-specific age thresholds marking the onset of actuarial
532 senescence. Information about age at first parturition, longevity and offspring sex is from data
533 analyzed here.

534

535 Table 2. Effects of the relative number of sons produced during early life on later lifespan for
536 females of four ungulate species. Interactions are denoted by ×.

537 Table 3. Effects of the relative number of sons weaned during early life on later lifespan for
538 females of four ungulate species. Interactions are denoted by ×.

539 Table 4. Effects of the relative number of sons produced during lifetime on maternal longevity
540 in four ungulate species. Interactions are denoted by ×. Sample sizes are larger compared to
541 previous analyses (table 2) because here we considered all adult females.

542 Table 5. Effects of the relative number of sons weaned during lifetime on maternal longevity
543 in four ungulate species. Sample sizes are larger compared to previous analyses (table 3)
544 because here we considered all adult females.

545

546

547 Table 1

Species	Soay sheep	Bighorn sheep	Mountain goat	Red deer
Population	Hirta	Ram Mountain	Caw Ridge	Rum
Start of the study	1985	1971	1988	1971
Onset of actuarial senescence	6 yr	7 yr	9 yr	9 yr
Early life	1-6 yr	2-7 yr	3-9 yr	3-9 yr
Mean age at first parturition (min, max)	1.5 yr (1, 6)	3.4 yr (2, 7)	4.7 yr (3, 8)	4.1 yr (3, 7)
Mean longevity for adults (sample size)	6.35 yr (N= 703)	9.4 yr (N= 173)	10.7 yr (N= 92)	12.2 yr (N=344)
Number of offspring of each sex at or shortly after birth	1783 ♀ 1762 ♂ 131 unknown	415 ♀ 392 ♂ 377 unknown	209 ♀ 204 ♂ 46 unknown	960 ♀ 967 ♂ 139 unknown

548 Table 2

549

Species	N	Effect	Slope	SE	Z	P
Soay sheep	357	No. offspring born early	0.040	0.017	2.32	0.02
		No. twins born early	-0.030	0.017	-1.81	0.07
		No. sons born early	-0.021	0.012	-1.84	0.06
		No. offspring born early × No. sons born early	0.016	0.009	1.71	0.09
Bighorn sheep	118	No. offspring born early	0.069	0.028	2.46	0.01
		No. sons born early	0.035	0.033	1.06	0.29
		No. offspring born early × No. sons born early	0.017	0.022	0.76	0.44
Mountain goat	59	No. offspring born early	0.003	0.025	0.14	0.89
		No. sons born early	0.001	0.025	0.03	0.98
		No. offspring born early × No. sons born early	0.011	0.022	0.52	0.61
Red deer	254	No. offspring born early	0.043	0.013	3.41	<0.001
		No. sons born early	-0.019	0.013	-1.48	0.14
		No. offspring born early × No. sons born early	0.005	0.010	0.54	0.59

550

551 Table 3

552

Species	N	Effect	Slope	SE	Z	P
Soay sheep	356	No. offspring weaned early	0.036	0.014	2.48	0.01
		No. twins weaned early	-0.029	0.015	-1.96	0.05
		No. sons weaned early	-0.018	0.011	-1.57	0.12
		No. offspring weaned early × No. sons weaned early	0.024	0.008	3.04	0.002
Bighorn sheep	115	No. offspring weaned early	0.009	0.028	0.32	0.74
		No. sons weaned early	0.058	0.028	2.04	0.04
		No. offspring weaned early × No. sons weaned early	0.007	0.021	0.35	0.73
Mountain goat	58	No. offspring weaned early	0.010	0.027	0.39	0.70
		No. sons weaned early	-0.004	0.028	-0.14	0.89
		No. offspring weaned early × No. sons weaned early	0.009	0.023	0.38	0.70
Red deer	254	No. offspring weaned early	0.031	0.013	2.28	0.02
		No. sons weaned early	-0.009	0.014	-0.62	0.53
		No. offspring weaned early × No. sons weaned early	-0.003	0.010	-0.31	0.76

553

554 Table 4

555

Species	N	Effect	Slope	SE	Z	P
Soay sheep	703	Lifetime no. offspring born	0.546	0.018	29.51	<0.001
		Lifetime no. twins born	-0.107	0.012	-8.98	<0.001
		Lifetime no. sons born	0.128	0.018	7.10	<0.001
		Lifetime no. offspring born × Lifetime no. sons born	-0.134	0.010	-13.11	<0.001
Bighorn sheep	173	Lifetime no. offspring born	0.331	0.022	15	<0.001
		Lifetime no. sons born	0.034	0.025	1.35	0.18
		Lifetime no. offspring born × Lifetime no. sons born	-0.033	0.014	-2.34	0.02
Mountain goat	92	Lifetime no. offspring born	0.263	0.027	9.62	<0.001
		Lifetime no. sons born	0.037	0.031	1.20	0.23
		Lifetime no. offspring born × Lifetime no. sons born	-0.056	0.016	-3.43	<0.001
Red deer	344	Lifetime no. offspring born	0.283	0.014	19.84	<0.001
		Lifetime no. sons born	0.070	0.015	4.60	<0.001
		Lifetime no. offspring born × Lifetime no. sons born	-0.104	0.010	-10.23	<0.001

556

557 Table 5

558

Species	N	Effect	Slope	SE	Z	P
Soay sheep	608	Lifetime no. offspring weaned	0.407	0.018	22.60	<0.001
		Lifetime no. twins weaned	-0.073	0.013	-5.78	<0.001
		Lifetime no. sons weaned	0.107	0.018	5.94	<0.001
		Lifetime no. offspring weaned × Lifetime no. sons weaned	-0.102	0.010	-10.34	<0.001
Bighorn sheep	165	Lifetime no. offspring weaned	0.253	0.032	7.85	<0.001
		Lifetime no. sons weaned	0.073	0.030	2.41	0.02
		Lifetime no. offspring weaned × Lifetime no. sons weaned	-0.041	0.019	-2.15	0.03
Mountain goat	84	Lifetime no. offspring weaned	0.197	0.032	6.22	<0.001
		Lifetime no. sons weaned	0.064	0.035	1.83	0.07
		Lifetime no. offspring weaned × Lifetime no. sons weaned	-0.047	0.018	-2.67	0.007
Red deer	325	Lifetime no. offspring weaned	0.330	0.015	15.12	<0.001
		Lifetime no. sons weaned	0.059	0.017	3.58	<0.001
		Lifetime no. offspring weaned × Lifetime no. sons weaned	-0.093	0.011	-8.79	<0.001

559

560 **Figure captions**

561 Figure 1. Predicted effects of the number of sons weaned during early life (1-6 years) on
562 lifespan (in years) for female Soay sheep that lived more than 6 years and a) produced 4 to 7
563 offspring (values within the 10-90 percentile range) during early life, b) weaned 3 to 6
564 offspring (values within the 10-90 percentile range) during early life. Circles are observed
565 lifespan in one of imputed data sets (see Methods). The size of the circle is proportional to the
566 number of females.

567 Figure 2. Predicted changes in longevity (in years) with the lifetime number of sons produced
568 (a, c, e, g) or weaning (b, d, f, h) relative to the lifetime number of offspring produced/weaned
569 according to each species, female Soay sheep (a, b), bighorn sheep (c, d), mountain goats (e,
570 f), and red deer (g, h). Each line represents predicted longevity for females with a different
571 number of offspring indicated at the end of the line. Predictions are shown between the 10^{th}
572 and the 90^{th} percentile of number of offspring. Circles are observed lifespan in one of imputed
573 data sets (see Methods). The size of the circle is proportional to the number of females.

574